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THE COPULATORY ORGANS OF THE CRYPTIC SPECIES *LYCOSA THORELLI* AND *LYCOSA CARBONELLI* AND THEIR HYBRID PROGENY, WITH NOTES ON THEIR TAXONOMY (ARANEAE, LYCOSIDAE)

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ABSTRACT. The copulatory organs of the cryptic species *Lycosa thorelli* and *Lycosa carbonelli* are studied and are shown to exhibit some differences. The morphology of the epigynum, vulva and palpal organs of *L. carbonelli* are here described for the first time. Additional morphological data of these species are provided and the specific diagnosis reformulated. Measurements indicated that the copulatory organs of *L. carbonelli* are larger than *L. thorelli*. Morphological comparison between the parental species and the hybrid progeny show that hybrids are intermediate in morphology and size. The reproductive isolation in these cryptic species and the inheritance of the sexual characters in the hybrid progeny are discussed.

Keywords: *Lycosa carbonelli*, *L. thorelli*, copulatory organs, taxonomy, hybrids

Lycosa thorelli (Keyserling 1877) and *Lycosa carbonelli* Costa & Capocasale 1984 are two cryptic species distinguished by their sexual behavior, mainly by their courtship behavior (Costa & Capocasale 1984). Additionally, the presence of thin hairs on tarsus I of the male of *L. thorelli* and the absence of such hairs in *L. carbonelli*, was the only morphological character found to differentiate these species. Only the copulatory organs of *L. thorelli* were described because Costa & Capocasale (1984) assumed there were no somatic differences with *L. carbonelli*. Pérez-Miles' (1985) morphometric study of these species using somatic characters established that *L. carbonelli* had leg and body dimensions statistically larger than *L. thorelli*. Costa and Francescoli (1991) experimentally obtained interspecific copulations between these species. Only one of these copulations successfully (with a large male of the smaller sized species and a small female of the larger sized species) resulted in hybrid progeny. They indicated that most of the unsuccessful interspecific copulations were possibly caused by slight mechanical incompatibility between the genitalia of the two species.

Copulatory organs have been widely recognized as useful tools in spider systematics, mainly to diagnose species. Recently, the genus *Lycosa* Latreille 1804 has been redescribed based on a review of some Paleartic species (Zyuzin et al. 2000) but the Neotropical species are poorly known. This lack of knowledge is especially great in cryptic species. In this study, we attempted to determine if the copulatory incompatibility between *L. thorelli* and *L. carbonelli* is caused by morphological differences of the sexual characters; and how hypothetical differences are segregated in the hybrid progeny. Simó et al. (1999) made a preliminary contribution indicating differences on genital morphology between these species.

METHODS

The specimens studied were the same as those used by Costa & Francescoli (1991), Costa et al. (1992) and Costa et al. (1997) in several experimental studies and identified on the basis of their sexual behavior. A total of 109 individuals of *L. thorelli* (29♂ & 20♀) and *L. carbonelli* (30♂ & 30♀) and 13 hybrids (7♂ & 6♀), was examined and deposited in the collection of Sección Entomología, Facultad de Ciencias, Montevideo (FCE). The SEM studies were made in the Laboratorio de Microscopía Electrónica del Museo de la Plata Argentina (MLP). The types examined are deposited in the following institutions: Museo

Nacional de Historia Natural de Montevideo (MNHN) and British Museum of Natural History, London (BMNH). The maximum length (LE) and width (WE) of the septum of the epigynum and the maximum length (LC) and width (WC) of the cymbium was measured, and their means compared with a Student's t-test. Copulatory organs were cleared in clove oil, and the bulbs were expanded with potassium hydroxide (KOH). The terminology used for the copulatory organs follows Sierwald (1989, 1990). For the Student t-test the significance level used was $P = 0.05$. All measurements are in millimeters. Abbreviations: BS = base of the spermatheca, CD = copulatory duct, FD = fertilization duct, HS = head of the spermatheca, SE = septum of the epigynum, TA = terminal apophysis.

RESULTS

Interspecific and parental-hybrid comparisons.—The most distinctive morphological interspecific gap found for females was the width of the septum of the epigynum (Figs.1, 4). The septum is narrower in *L. thorelli* (0.15 ± 0.03 mm, n = 18) than in *L. carbonelli* (0.29 ± 0.06 mm, n = 17); the statistical comparison resulted in significant differences ($t = 5.26$, $P < 0.001$). Hybrids have intermediate values of septum width (0.22 ± 0.03 mm, n = 6), and comparisons with both parental species also showed significant differences: $t = 3.9$, $P < 0.001$ with *L. carbonelli* and $t = 4.25$, $P < 0.001$ with *L. thorelli*. Vulvae did not show very clear interspecific differences (Figs. 2, 5). In males the main interspecific difference was the presence of a curved terminal apophysis in the palpal organ of *L. thorelli*, which is straight in *L. carbonelli* (Figs. 3, 6).

Significant differences were found for all other measurements between the parental species studied: LE, $t = 7.48$, $P < 0.001$; LC, $t = 5.81$, $P < 0.001$; WC, $t = 8.21$, $P < 0.001$. In all cases the analyzed features of the copulatory organs of *L. carbonelli* were significantly larger than in *L. thorelli* ($P < 0.001$). Respectively the means (± standard deviation) for *L. carbonelli* and *L. thorelli* were LE: 0.74 (± 0.04), 0.63 (± 0.05); LC: 1.88 (± 0.15), 1.59 (± 0.15), WC 1.02 (± 0.08), 0.83 (± 0.07).

Comparisons of the measurements of the copulatory organs between the hybrids and each of the parental species showed significant differences between the hybrids and *L. carbonelli* for all the characters compared (in all cases $P < 0.001$). In comparisons between hybrids and *L. thorelli* no significant differences were found for WC and LC, but the comparisons of WE (as mentioned above) and LE ($P < 0.001$) showed significant differences.

Tarsal dorsal hair of leg I, indicated as diagnostic of *L. thorelli*, was found also in *L. carbonelli* (Fig. 7) and in their hybrid progeny. On the basis of the present results we rediagnose the species below.

Lycosa thorelli (Keyserling 1877)
Figs. 1–3

Tarentula thorelli Keyserling 1877:650; Keyserling 1891:257.

Tarentula sternalis Bertkau 1880:73.

Lycosa thorelli: Petrunkevitch 1911:568; Bonnet 1957:2629; Zimber 1963:19; Capocasale 1980: 65; Costa 1980:67; Costa & Capocasale 1984: 428; Pérez-Miles 1985:19; Gudynas & Pérez-Miles 1988:1; Costa & Francescoli 1991:1768; Francescoli & Costa 1992:380; Platnick 1993: 489; Platnick 1997:560; Costa et al. 1997:1845; Costa et al. 2000:237.

Lycorma thorelli: Roewer 1954:267

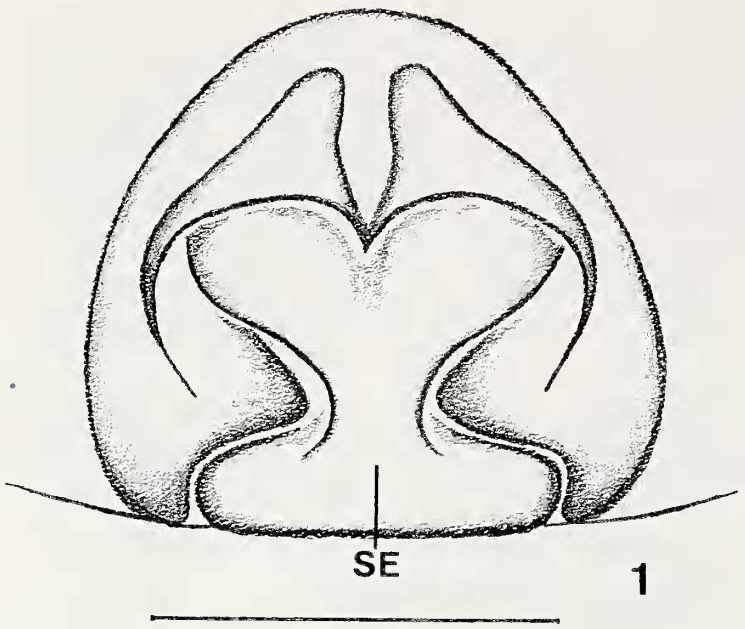
Types.—Two females and one male (syntypes) from Colombia, 1890.7.1.2600–15, examined, deposited in BMNH.

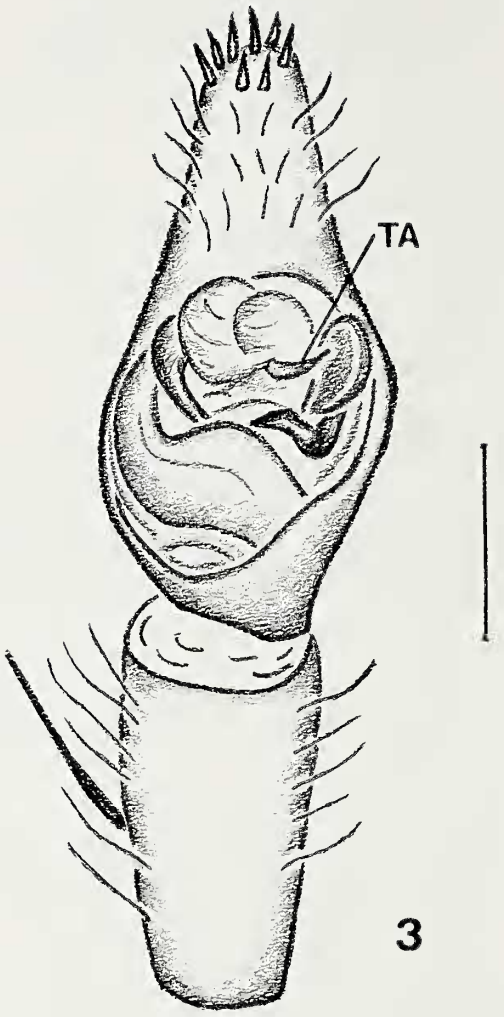
Diagnosis.—Differs from *L. carbonelli* by the intensification of the alternate waving of the forelegs during the second precopulatory phase (see Costa & Francescoli 1991), the presence of a narrow septum on the epigynum (Fig. 1) and by the presence of a curved terminal apophysis (Fig. 3).

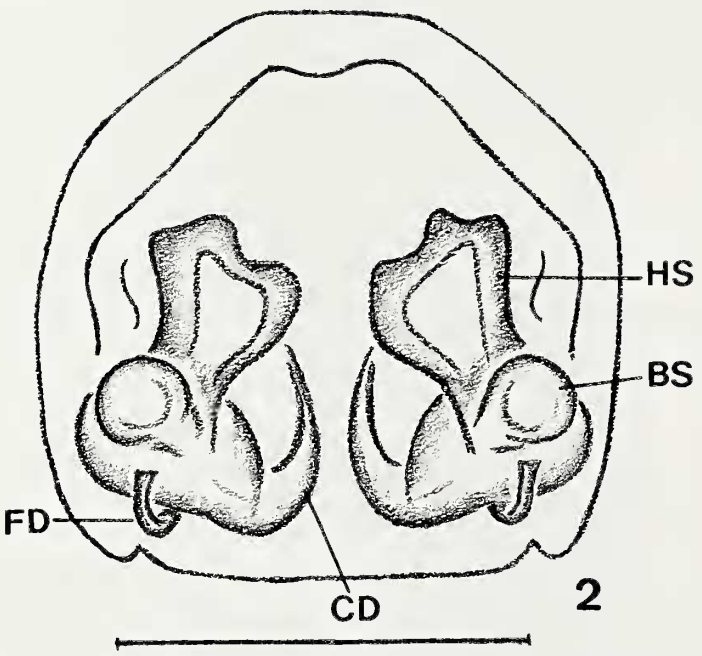
Additional material examined.—URUGUAY: *Canelones*; Marindia, 17 November 1996 (Costa, FCE) 1♂; 17 December 1996 (Costa, FCE) 1♂; 11 May 1998 (Costa, FCE) 2♀; 8 October 1998 (Costa, FCE) 3♂; 23 October 1998 (Costa, FCE) 1♀. Rocha. Bocas del Sarandí: 26 August 1994 (Pérez-Miles & Toscano, FCE) 6♀. Sarandí del Consejo, 23 July 1994 (Pérez-Miles & Toscano, FCE) 1♂; 30 September 1994 (Pérez-Miles & Toscano, FCE) 1♀. Potrero Grande: 21 July 1994 (Pérez-Miles & Toscano, FCE) 3♀, 2♂.

Lycosa carbonelli Costa & Capocasale 1984
Figs. 4–7

Lycosa carbonelli Costa & Capocasale 1984:426; Pérez-Miles 1985:19; Gudynas & Pérez-Miles







Figures 1–3.—*Lycosa thorelli* copulatory organs, 1. Epigynum; 2. Vulva; 3. Pedipalp, ventral view. Scale = 0.5 mm.

1988:1; Costa & Francescoli 1991:1768; Francescoli & Costa 1992:380; Platnick 1989:370; Platnick 1993:489; Platnick 1997:560; Costa et al. 1997:1845; Costa et al. 2000:237.

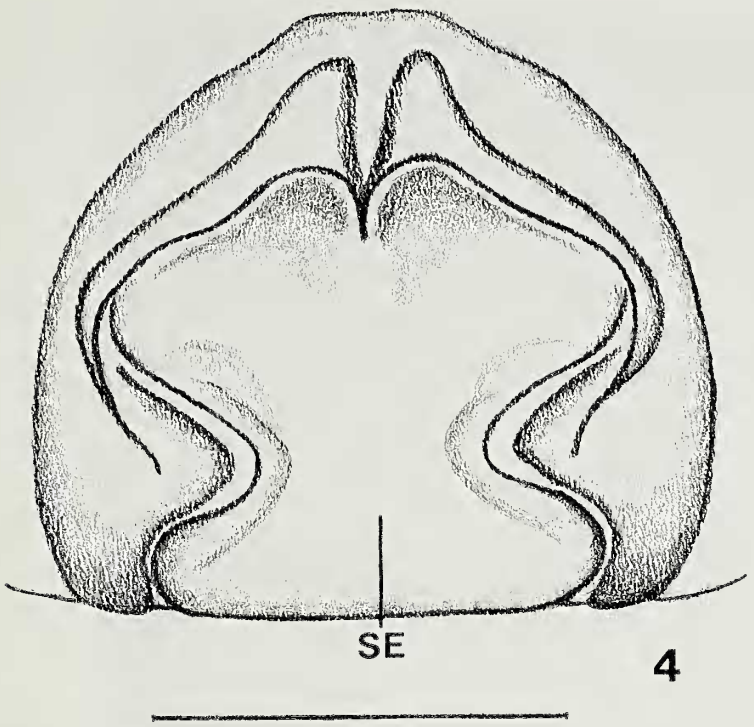
Types.—Male holotype and paratype female from Malvín, Montevideo, (750), May 1977, F. Costa Col., examined, deposited in MNHN.

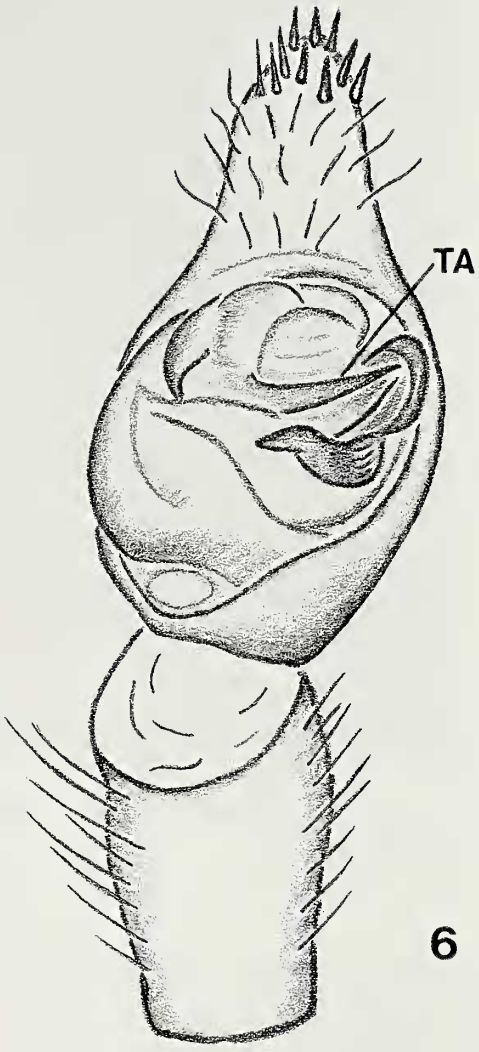
Diagnosis.—Differs from *L. thorelli* by the alternation of "explosive" locomotion with prolonged immobility at the second precopulatory phase (see Costa & Francescoli 1991), the broad septum on the epigynum (Fig. 2) and by the presence of a straight and longer terminal apophysis (Fig. 6).

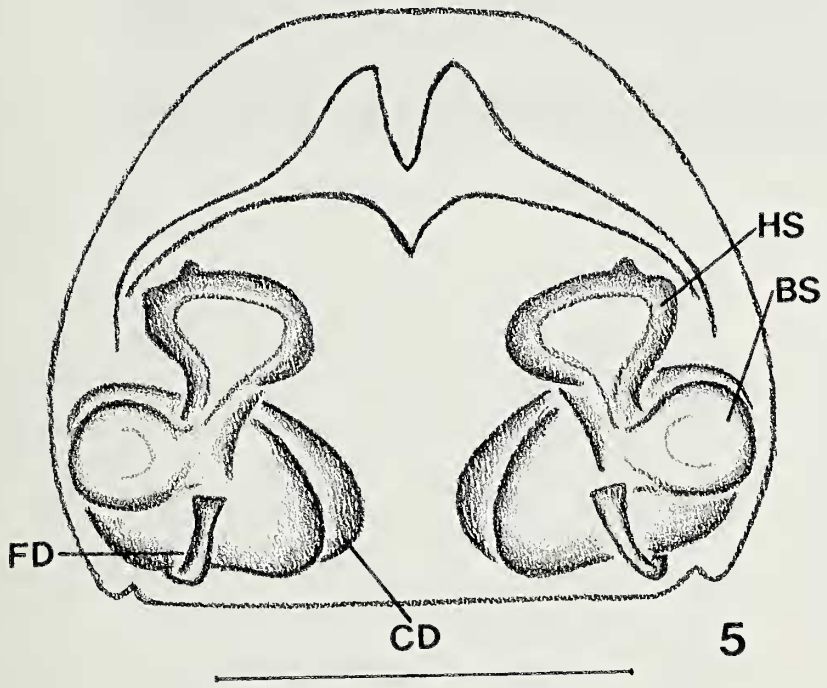
Additional material examined.—URUGUAY: *Canelones*; Marindia, 11 May 1998 (Costa, FCE) 4♂; 25 June 1998 (Costa, FCE) 1♀; 18 October 1996 (Costa, FCE) 1♀; 23 October 1998 (Costa, FCE) 2♀.

DISCUSSION

Stratton & Uetz (1981, 1997) studied three cryptic species of *Schizocosa* Chamberlin 1904 obtaining hybrids in forced copulations. They indicated the importance of courtship isolation mechanisms among these species. Töpfer-Hofmann et al. (2000) studied six closely related cryptic species of *Pardosa* Koch 1847 from Europe. They found that courtship behavior was the main isolating mechanism in at least five of these species. The females could not be reliably distin-







Figures 4–6.—*Lycosa carbonelli* copulatory organs, 4. Epigynum; 5. Vulva; 6. Bulb, ventral view. Scale = 0.5 mm.

guished by their somatic or genitalic characters.

In the two cryptic species studied here, the only morphological difference indicated by Costa & Capocasale (1984) for distinguishing them was the presence of thin hairs on tarsi I of the male of *L. thorelli*, and their absence in *L. carbonelli*. Since we found these hairs in both species we remove it as diagnostic character.

Francescoli & Costa (1992) studied the post-emergence development of *L. carbonelli*, *L. thorelli* and their hybrid progeny. They found that the duration of the development of the hybrids was intermediate between the parental species, although it was closer to the duration of *L. carbonelli*. In another study, Costa et al. (1997) analyzed the male sexual behavior elicited by a hybrid pheromone, using specimens of *L. carbonelli*, *L. thorelli* and hybrids. They found that hybrid males showed behaviors similar to those of each of the parental species, but their characteristics (units frequency, angle covered by leg movement and standardized duration) were intermediate between the two. Results obtained here show that the morphology of the copulatory organs in hybrids is slightly more related to *L. car-*

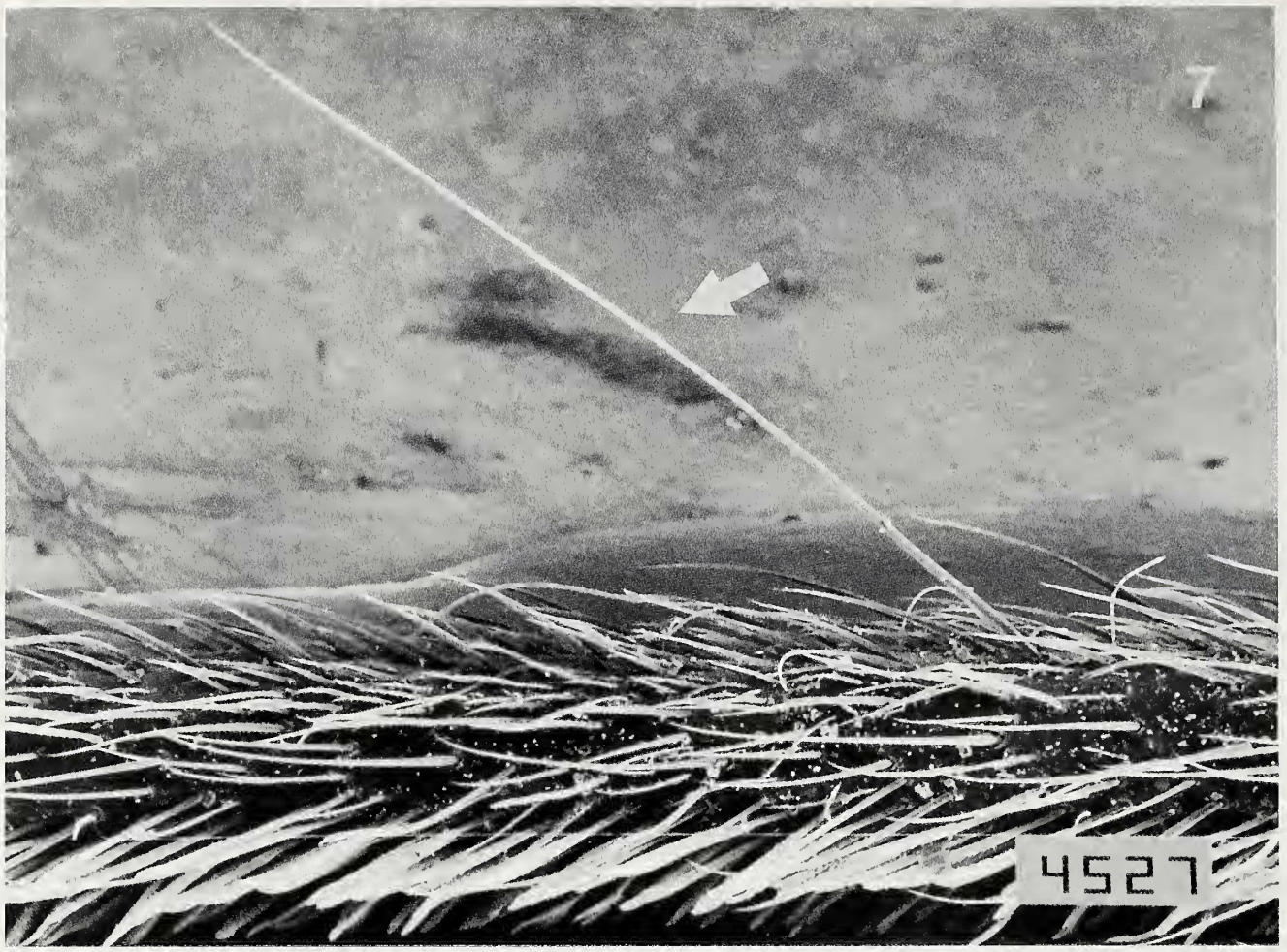


Figure 7.—Left male tarsus I of *Lycosa carbonelli*. The arrow shows one longer hair (see text). 100X. Scale = 1000 μm.

bonelli. The width of the epigynal septum seems to be a good diagnostic character to distinguish between the species and showed intermediate values in hybrids. These results suggest the polygenic inheritance of such ethological and morphological characters. The mechanical incompatibility between the copulatory organs of *L. carbonelli* and *L. thorelli* indicated by Costa & Francescoli (1991) could be explained by the morphological and morphometric differences demonstrated here.

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